

# The upper temporal arcade of lizards: an ontogenetic problem

by

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With 3 figures

## ABSTRACT

The skull of miniaturized and fossorial lizards is distinctly modified as compared to that of more typical lizards. The role of ontogeny in the formation and modification of dermatocranial structures is investigated. The general deficiency of knowledge with respect to the postnatal differentiation and growth of the lizard skull is highlighted.

## INTRODUCTION

The upper temporal arcade of the lizard skull is formed by the postorbital and postfrontal anteriorly and by the squamosal posteriorly. The first two bones may fuse, or the postorbital may be absent. In a variety of lizards the upper temporal arcade is incomplete and some or all of its constituent bones may be lost. These lizards are the Gekkota, some Scincidae (*Acontinae*), *Dibamus* and *Anelytropsis*, the anguid lizard *Anniella* and the platynotan genera *Heloderma* and *Lanthanotus*. The upper temporal arcade has been lost convergently in a variety of lizards, probably for more than one functional reason.

My work has concentrated on the head anatomy of miniaturized fossorial or burrowing lizards of various families including the Pygopodidae (*Aprasia* and *Pletholax*: RIEPPEL, in press), Scincidae (*Acontias*, *Acontophiops* and *Typhlosaurus*: RIEPPEL, 1981, 1982), Anguidae (*Anniella*: RIEPPEL 1980a) and Dibamidae (*Dibamus*: RIEPPEL, in prep.). In all of these lizards a convergent pattern of modification of the head anatomy is observed. The upper temporal arcade is incomplete. Its anterior element, the postorbito-frontal, usually persists and braces the potentially movable (mesokinetic) fronto-parietal suture laterally (with the exception of *Dibamus*). Of the squamosal, only the posterior

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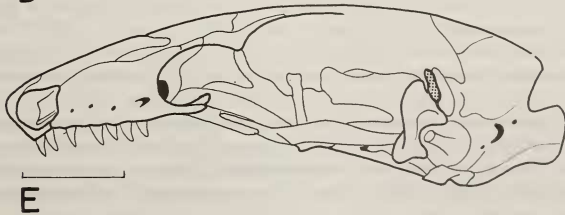
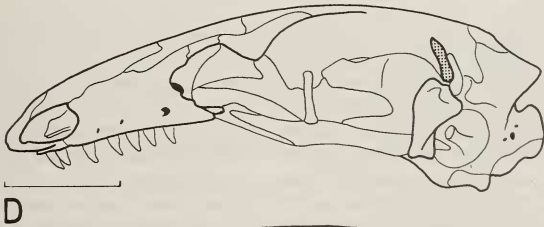
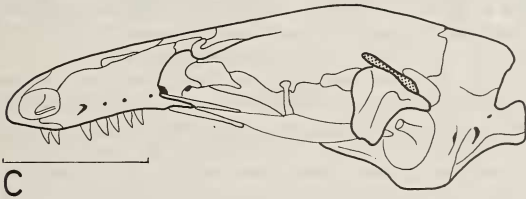
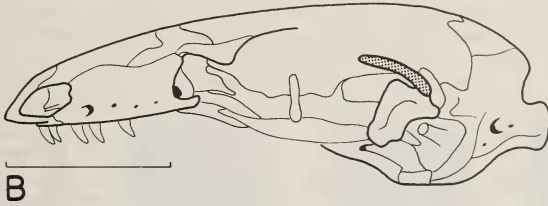
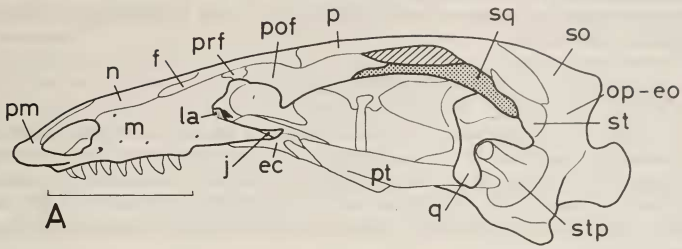
part persists which takes part in the quadrate suspension (the squamosal is completely reduced in at least two species of *Aprasia*, in *Anniella* and in *Dibamus*). The parietal develops extensive lateral downgrowths which together with the prootics from closed lateral braincase walls from which the jaw adductor muscles take their origin. Those layers of the external adductor which primitively take their origin from the upper temporal arcade (HAAS 1973) and from the fascia which covers the upper temporal fenestra now take their origin from the lower surface of an extensive temporal fascia which is attached to the parietal dorsally. These fibres also show a characteristic extension of their origin in a posterodorsal direction to what SÄVE-SÖDERBERGH (1945) termed the "temporalis position".

## THE PROBLEM

One question to be asked in relation to the problem of miniaturization in fossorial lizards concerns the mode of reduction of the upper temporal arcade. The investigation of the scincid genus *Typhlosaurus* (RIEPEL 1981, 1982) resulted in an almost complete morphocline documenting the reduction of the squamosal from front to back. *Typhlosaurus lineatus* (Fig. 1A) retains a complete upper temporal arcade which has, however, closely approached the parietal, thus minimizing the diameter of the head and hence the work required to push the head through the substrate. The upper temporal fenestra consequently is of small size. In the other species of the genus the upper temporal arcade is incomplete. The postorbitofrontal is retained as a V-shaped element of variable size. The squamosal is closely applied to the lateral parietal downgrowth, and it is progressively reduced from front to back (Fig. 1A). Such a morphocline is an idealistic representation of graded similarities of form (DULLEMEIJER 1974). Its use as a model for phylogenetic processes is not unproblematical, but nevertheless the morphocline is suggestive of an ontogenetic mechanism controlling the reduction of the squamosal. If the squamosal can be shown to develop from its posterior portion in an anterior direction in the course of ontogeny of lizards in general, then the reduction of the bone from front to back as observed in *Typhlosaurus* can be explained by paedomorphosis, defined as "the retention of ancestral juvenile characters by later ontogenetic stages of descendants" (GOULD 1977: 484). Conversely, the development of extensive parietal downgrowths is due to hypermorphosis of the parietal. Hypermorphosis was defined by GOULD (1977: 482) as "the phyletic extension of ontogeny beyond its ancestral termination...". Indeed, GOULD (1977: 332) discusses miniaturization by progenesis as an adaptive response to selection pressures for small size in invertebrates, while TRUEB & ALBERCH (1983) have shown that cranial bones lost in miniaturized anurans are "elements that appear late in ontogenetic development". Changes of the timing of developmental events are also involved in the pattern of miniaturization of the pletho-

FIG. 1.

The skulls of five species of *Typhlosaurus* in left lateral view to show the reduction of the squamosal. A: *T. lineatus*; B: *T. vermis*; C: *T. braini*; D: *T. aurantiacus*; E: *T. cregoi*. Abbreviations: ec, ectopterygoid; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; op-co, opisthotic-exoccipital; p, parietal; pm, premaxilla; pof, postorbitofrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; st, supratemporal; stp, stapes. Scale lines equal 2 mm. (From *Annals Transvaal Mus.* 33 (12): 253, Fig. 4. By permission of the editor).



dontid salamander genus *Thorius* (HANKEN 1980). In all these cases, however, modifications by changes of developmental patterns are limited by functional constraints (TRUEB & ALBERCH 1983).

## INVESTIGATIONS

The study of development of the osteocranium in lizards is extremely incomplete, being essentially restricted to the description of the osteocranium of late embryos or hatchlings of a few taxa such as *Lacerta*, *Mabuyia*, *Chalcides*, *Acontias* and *Ptyodactylus* (BELLAIRS & KAMAL 1981). Knowledge of the postnatal development of the osteocranium is even more deficient. Here opens a wide field for future research (BELLAIRS & KAMAL 1981: 4).

In *Lacerta* the development of the squamosal starts from the posterior end. The bone arises "off the lateral surface of the auditory capsule, beneath and in front of the supratemporal, above the dorsal end of the quadrate and behind the postorbital" (deBEER, 1937: 232). Consequently it must grow anteriorly in order to develop its adult shape. In the gecko *Ptyodactylus hasselquistii* the squamosal again arises as a small splint of bone dorsal to the cephalic condyle of the quadrate (EL-TOUBI & KAMAL 1961: Fig. 1; the squamosal is considered as a supratemporal or tabular by these authors, but see the discussions of the homology of the single temporal bone in geckos by UNDERWOOD 1957, and KLUGE 1967). In a late embryo of the scincid species *Chalcides ocellatus* (EL-TOUBI & KAMAL 1959) the upper temporal arcade is already essentially completed. In a hatchling of *Calotes versicolor* only the posterior portion of the squamosal is developed. The bone has not yet established the contact with the postfrontal (RAMASWAMI 1946: Fig. 16). The conclusion then seems safe that the squamosal of lizards develops ontogenetically from its posterior portion in an anterior direction. The pattern of squamosal reduction in the genus *Typhlosaurus* can thus be explained by paedomorphosis.

An interesting problem, however, arises from the fact that in lizard hatchlings the upper temporal arcade can be completely developed while the skull roof is only beginning to ossify. In the late embryo of *Chalcides ocellatus* investigated by EL-TOUBI & KAMAL (1959) the squamosal has already established contact with the postorbital, while of the frontal and parietal bones only the marginal zones have ossified. The postfrontal is not yet fully formed. Similar observations hold for a late embryo of *Ptyodactylus hasselquistii* described by EL-TOUBI & KAMAL (1961). Again only the marginal zones of the parietal have ossified, as is also the case in hatchlings of *Calotes versicolor* (RAMASWAMI 1946) and of *Podarcis muralis* (Fig. 2). In the hatchling of *Podarcis muralis* the upper temporal arcade is essentially complete, whereas the parietal is ossified along its marginal zones only. During postnatal growth the postfrontal extends a little further caudally, while the parietals complete ossification and during this process fuse to form a single element. The parietal unit, including the upper temporal arcade, is part of the linkage system which makes up the kinetic lizard skull (FRAZZETTA 1962). This linkage system must be functional at the hatchling stage, and the parietal unit is represented by a three dimensional framework around the braincase at this stage. Moreover, those jaw adductor muscles of *Lacerta/Podarcis* (described by RIEPPEL 1908b), which do not originate from braincase or palatoquadrate elements, take their origin from the lower surface of the postfrontal, postorbital and squamosal, from the marginal zone of the parietal and from the dorsal margin of the posttemporal fossa, i.e. from the lower surface of the supratemporal process of the parietal. These are the parts of the dermal parietal unit which are ossified in the hatchling, obviously for functional reasons.

It has been demonstrated that the growth of bone, e.g. of the mammalian mandible, is controlled or influenced by the muscles and the mechanical stimulations they provide DULLEMEIJER 1971: 64; 1974; FROST 1964: 32-33; HALL 1978: 219-221). MOSS (1960) introduced the term "functional matrix" to denote all those factors and influences which mould the bony element. Muscles are one of these factors. DULLEMEIJER (1974: 134f) criticizes Moss' terminology as it implies a subordination of the bony element to the

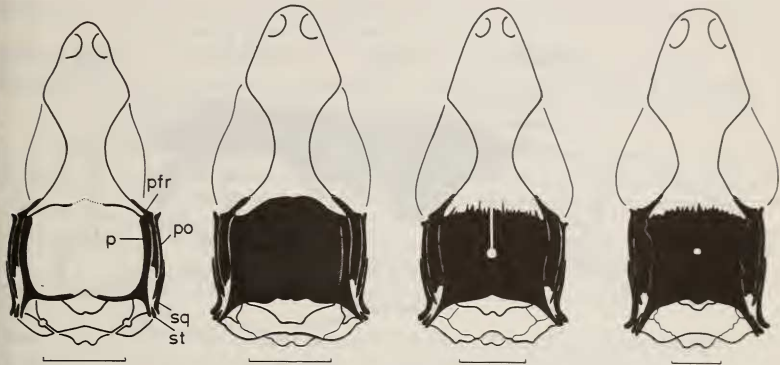


FIG. 2.

The postnatal development of the parietal unit in *Podarcis muralis* (MBS 21369 a-d; semidiagrammatic). Abbreviations: pfr, postfrontal; po, postorbital; others as in Fig. 1. Scale lines equal 2 mm.

functional matrix and thus precludes the possibility of an effect of the skeletal unit on muscle differentiation. In view of these problems it would be interesting to investigate at which stage of ontogeny and ossification of the cranial bones the muscles become attached to these in lizards. Also, the functional interdependence of muscles and bones presupposes some correlation between the pattern of ossification in the developing skull and the development of the musculature which would be interesting to investigate.

## CONCLUSIONS

### PATTERNS OF SKULL MODIFICATION IN MINIATURIZED LIZARDS

In the lizards investigated the dermal skull roof is not yet fully developed in the hatchling. Only the elements of the upper temporal arcade and the marginal zones of the parietal are fully ossified. These elements are functionally important since they form part of the kinetic linkage system of the lizard skull and serve as sites of muscle origin.

These observations stand in marked contrast to what little is known about the skull development in miniaturized fossorial lizards. BROCK (1941) described the only late embryo of *Acontias meleagris* that has so far become available (Fig. 3). *Acontias* is closely related to the genus *Typhlosaurus*, the two genera being united within a subfamily of the Scincidae, the Acontinae (GREER 1970; RIEPPEL 1982). A late embryo was also included in BELLAIRS' (1950) study of the head anatomy of *Anniella*. In the late embryo of *Acontias* described by BROCK (1941) the parietal downgrowths are well developed

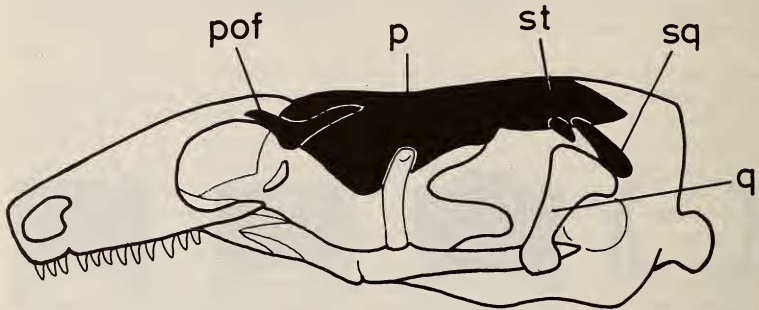


FIG. 3.

The skull of a late embryo of *Acontias meleagris* (after BROCK 1941, Fig. 5).  
Abbreviations as in Fig. 1.

but not yet complete at their ventral margins (Fig. 3). Drawings of cross-sections indicate that the ossification of the dorsal aspect of the parietal is complete (BROCK 1941: Fig. 8). Only the posterior part of the squamosal is present as will also be the case in the adult. The postorbitofrontal has essentially completed its development. BELLAIRS' (1950) description of *Anniella* does not contradict these findings as far as the development of the parietal is concerned. The advanced development of the parietal in these fossorial and miniaturized lizards may be correlated with the differentiation of the jaw adductor musculature which originates from the parietal downgrowths or from a temporal fascia which is anchored to the dorsal aspect of the parietal. In fact, the *Bauplan* of the skull has changed. The dermatocranium no longer forms a kinetic framework within which the neurocranium is movably suspended as in typical lizards. Rather the dermatocranium and neurocranium combine to form a solid central strut from which the jaws are movably suspended. If the jaws and their muscles are to be functional in the hatchling, the central strut of the skull which supports them must be well developed at that stage.

In conclusion it might be said that the reduction of the squamosal from front to back in lizards such as *Typhlosaurus* can in fact be explained by paedomorphosis. Paedomorphosis with respect to the development of the elements of the upper temporal arcade and acceleration of the development of the parietal represent ontogenetic mechanisms by which the structural and functional alterations in the skulls of miniaturized and fossorial lizards are achieved.

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